POPULATION STRUCTURE AND ONE-YEAR DYNAMICS OF THE ENDANGERED TROPICAL TREE SPECIES *CAESALPINIA ECHINATA* LAM. (BRAZILIAN RED-WOOD): THE POTENTIAL IMPORTANCE OF SMALL FRAGMENTS FOR CONSERVATION

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ABSTRACT

(Population structure and one-year dynamics of the endangered tropical tree species *Caesalpinia echinata* Lam. (Brazilian red-wood): the potential importance of small fragments for conservation) *Caesalpinia echinata* Lam. an endangered species, occurs in forest fragments of the Cabo Frio region, in Rio de Janeiro, Brazil. Data from four sub-populations were used to describe local population patterns and one-year dynamics. In each subpopulation, 0.1 ha-plots were set up and all *C. echinata* trees were mapped, and diameter and height were measured. The fragments sampled had different sizes and were subjected to various degrees of man-made disturbance, representing a succession gradient from an earlier (small fragment) to a later stage (large fragment). We compared the sub-populations as regards density, size structure, spatial distribution, germination and mortality, to identify short-term responses to mechanical injuries (broken stems, sand burial and man-made cuts). Matrix analysis considering the four *C. echinata* sub-populations together showed a slight tendency for population expansion ($\lambda = 1.0211$) if injury patterns do not lead to habitat extinction. On the other hand, sub-populations showed aggregated distribution patterns, particularly at forest edges. Diameter size structure varied from a reversed-J pattern, *i.e.* seedling abundance in the small fragment (more impacted sub-population) to a uniform plant distribution of size classes in the large one (less impacted sub-population). The sub-population in the smallest fragment showed the highest birth and mortality, in contrast to reduced demographic variation in the largest fragment. Moreover, the smallest fragment also showed the largest seedling stand density and biomass. These data indicate the potential importance of small fragments for the conservation of the Brazilian red-wood.

Key words: Atlantic forest, Cabo Frio region, fragmentation, population structure, matrix analysis.

RESUMO

(Estrutura populacional e dinâmica de um ano da espécie ameaçada *Caesalpinia echinata* Lam. (pau-brasil): a importância potencial de pequenos fragmentos para conservação) *Caesalpinia echinata* Lam. (pau-brasil) é uma espécie ameaçada de extinção que ocorre em fragmentos florestais da região de Cabo Frio no Rio de Janeiro. Quatro sub-populações da região foram utilizadas para detecção de padrões populacionais e estudo de um ano de dinâmica da espécie. Em cada uma destas sub-populações, parcelas de 0,1 ha foram estabelecidas e todos os indivíduos de *C. echinata* foram mensurados quanto ao diâmetro e altura. Os fragmentos selecionados possuíam tamanhos distintos e estavam sujeitos a impactos antropogênicos diferenciados. Tais impactos representaram gradientes de sucessão de estágios iniciais (fragmento pequeno) até estágios tardios (fragmento grande). As sub-populações foram comparadas quanto à densidade de indivíduos, estrutura de tamanhos, distribuição espacial, germinação e mortalidade, a fim de detectar respostas em curto-prazo das plantas aos danos mecânicos (quebra, soterramento e corte). Análises de Modelos Matriciais foram realizadas considerando as quatro sub-populações como uma única população local. Estas indicaram pequena tendência de expansão populacional após eventos reprodutivos ($\lambda = 1,0211$), caso os padrões de danos não conduzissem a extinção total do habitat. Paralelamente, as sub-populações exibiram padrões agregados de distribuição, especialmente nas bordas florestais. A estrutura de diâmetros variou desde o padrão de J-reverso, *e.g.* abundância de sementes no fragmento pequeno (sub-população mais impactada) até a distribuição uniforme observada nas classes de diâmetros do maior fragmento (sub-população menos impactada). A sub-população do menor fragmento exibiu as maiores taxas de nascimento e mortalidade, contrastando com a reduzida variação demográfica do maior fragmento. Entretanto, o menor fragmento também exibiu a maior densidade de plântulas e biomassa. Estes resultados indicam que pequenos fragmentos também são importantes para a conservação do pau-brasil.

Palavras-chave: Mata Atlântica, Cabo Frio, fragmentação, estrutura de populações, modelos matriciais.

INTRODUCTION

Increasing forest fragmentation creates even more small fragments, which often modify species distribution and abundance (Laurance *et al.* 1998; Fahrig 2003; Harper *et al.* 2005). For instance, the smaller the fragment the worse the deleterious edge effect (Janzen 1983; Laurance 2000). Among the most reported consequences are decline in seedlings of shade-tolerant species (Benitez-Malvido 1998) and biomass (Laurance *et al.* 1997), and changes in vegetation structure (Didham & Lawton 1999; Williams-Linera 1990; Laurance *et al.* 2001) and dynamics (Oliveira-Filho *et al.* 1997; Laurance *et al.* 2002, 2007). Since species populations often consist of series of sub- or local populations with a naturally fragmented distribution (Hanski & Gilpin 1991), habitat fragmentation and loss are further divisive forces that contribute to the decline of population density and lead to species extinction (Sih *et al.* 2000).

However, species can respond in different ways to man-induced environmental changes and a variety of responses related to mortality and recruitment is cited for distinct types of impact and of biological conditions (Lieberman *et al.* 1985; Condit *et al.* 1995; Bruna *et al.* 2002). Therefore, studies on population dynamics are an important tool for species conservation (Ehrlén & Groenendael 1998). This type of study often demands long-term efforts, particularly in the case of long-lived species such as many tropical trees, which is in contrast with the high speed of deforestation many habitats are currently facing (Myers *et al.* 2000), especially the tropical dry forests (Mooney *et al.* 1995; Sanchez-Azofeifa *et al.* 2005).

This is the case of *Caesalpinia echinata* Lam, a long-lived tropical tree which is rare and extremely threatened with extinction (*sensu* Schemske *et al.* 1994) according to Brasil (1992). Some of the last natural remnant populations of the Brazilian southeast are found in the Cabo Frio region in Rio de Janeiro state. This is a very fragmented Centre of Plant Diversity (Araujo 1997) and pointed out as the habitat of the most genetically diverse and preserved *C. echinata* population in southeastern Brazil (Cardoso *et al.* 2005). Therefore, long-term studies on population dynamics of this species would be essential for conservation planning. However, the absence of conservation units to protect this species and the still very high deforestation rates, due to land speculation and predatory tourism, call for urgent initiatives and hinder long-term studies. Hence, in this study we tried to identify general population patterns and short-term relationships between damage, local survival and regeneration of the Brazilian red-wood in forest fragments. We use size structure data and one year dynamics from 4 sub-populations in neighbouring sites that represent a gradient from an earlier (small fragment) to a later (large fragment) succession stage (see McCook 1994), due to previous human activity. Our premise is that a short-term structural study to compare different succession stages within this spatial gradient helps provide an understanding of long-term population dynamics.

MATERIAL AND METHODS
Studied species

Caesalpinia echinata Lam. (Leguminosae-Caesalpinoideae) is a tree species that can reach heights of up to 10–20 m, rarely 30 m, and is typical of the Brazilian coastal plain forest. It was originally distributed abundantly in seasonal semideciduous vegetation patches, with sclerophyllous appearance, along the Brazilian Atlantic coast between the northeastern state of Rio Grande do Norte and São Paulo state in the southeast. Nowadays, however, only small native populations can be found (Cunha & Lima 1992).

The Brazilian red-wood has suffered predatory exploitation during the past 500 yrs. Its harvest was an important economic activity because of the red colour extract used to tinge clothes (Corrêa 1974). The chemical production of pigments finished this overexploitation, but too late to avoid the near extinction of the species. The tree is currently grown commercially

in some parts of the country, and the wood is exported for the production of high quality violin bows (Cunha & Lima 1992).

Study area

The study area (22°48'S–41°58'W) is located in the state of Rio de Janeiro between Cabo Frio and Armação de Búzios municipalities (Cabo Frio region). This site is a semideciduous forest where *C. echinata* is among the dominant species (Geβler *et al.* 2005). This forest is part of the so-called Atlantic forest complex (see Oliveira-Filho & Fontes 2000; Scarano *et al.* 2001; Scarano 2002), which has been reduced to less than 7% of its original area, thus consisting of one of the world's most important biodiversity hotspots (Myers *et al.* 2000). The climate according to the Köppen system corresponds to a variation of Hot-arid (Bsh) contrasting with the predominantly rainy climate of the rest of the state. Rainfall is around 800 mm/year, with less than 80 mm/month. Dry season is from June to August, with ca. 40 mm/month (FEEMA 1988).

Sub-populations of *C. echinata* were sampled at the following sites: a) a small fragment (SF; ca. 0.2 ha); b) a hillside fragment (HF; ca. 2.5 ha); c) the centre (CF) and d) the edge (EF) of a large fragment (ca. 10 ha). SF lies between an unpaved road and a pasture. The canopy is dominated by a large *C. echinata* tree (ca. 15 m tall), which provides shade for most of the fragment. However, a pronounced edge effect, in addition to canopy gaps, allows for light penetration in the understory, where climbers occur abundantly. Moreover, trampling by cattle commonly takes place, given that this fragment is not fenced. HF is on a hillside and its canopy reaches ca. 9m tall. CF and EF are located in a dense, mature, dry forest remnant (ca. 10 ha) bordered by pastures, occasionally invaded by cattle. CF is a sub-population deep inside (200 m from the edge) the forest and EF was at the edge of the forest (from the edge to 30 m inwards). For structural analysis we considered CF and EF as distinct sub-populations due to the absence of individuals

of *C. echinata* between these two groups and the obvious environmental differences between edge and centre of this forest fragment. For dynamic analysis we considered the four sub-populations together. Canopy plants reached ca. 10 m with emergent ones, like *C. echinata*, reaching heights of 15 m.

Population sampling and data analyses

A 0.1-ha plot (20 m × 50 m) was established in each sub-population site between June and August 1996. The plots were subdivided into forty 5 × 5 m quadrats. Each specimen of *C. echinata* was labelled, mapped and measured for basal diameter (bd) and height (h). Mechanical injuries, such as broken stems, sand burial, resprouting and man-made cuts, were recorded. After one year, all individuals were measured and observed again. Seedlings germinated in November 1997 (3 months after the 1997 re-sampling) were sampled inside ten 1 m × 1 m plots randomly placed in a circle (20 m radius) which had at its centre one reproductive adult, at each of the four sub-population sites. Spatial distribution patterns were determined using Morisita's Standardized Dispersion Index (Krebs 1989).

Biological diameter classes

Basal diameter (bd) classes were defined based on biological characteristics of the plants. Thus, seedling stage 1 (bd $\leq$ 5 mm) showed the first leaves and a thin, brown stem. Seedling stage 2 (5 mm < bd $\leq$ 10 mm) had more leaves and a thin stem tending to grey (due to lichen colonization) with small thorns. Sub-saplings (10 mm < bd $\leq$ 20 mm) and saplings (20 mm < bd $\leq$ 30 mm) had thorny, woody stems, grey and with old apical meristem scars. Sub-adults (30 mm< bd $\leq$ 60 mm) were trees that did not flower during the reproductive season of 1997. Small adults (60 mm < bd $\leq$ 150 mm) were emergent trees that flowered at the hillside fragment. Adults (bd > 150 mm) flowered and often occupied the emergent *stratum*.

The sum of diameters of all individuals in each sub-population was used to obtain the

basal area (m²). One-way analysis of variance was used to assess differences between population size structures in 1997 of seedlings (bd < 20 mm), saplings (20 mm < bd ≤ 60 mm) and adults (bd > 60 mm). Spojtvoll/Stoline Tukey's tests were used to compare mean values of these categories (Sokal and Rohlf 1995).

Whole-population patterns

A transition matrix model as described by Lefkovitch (1965) and modified by Caswell (1989) was used to analyze *C. echinata* population dynamics. All sampled sub-populations were treated here as a unique population, which was a legitimate approach as demonstrated by molecular biology studies (Cardoso *et al.* 2005). The matrix is of the form: $n_{t+1} = A \times n_t$. where A is a square matrix containing transition probabilities among categories during one time-step and n is a vector containing the number of individuals in each category at time t and $t+1$. This equation assumes that environmental factors are constant in time and the population structure at time $t+1$ is obtained by multiplying the structure at time t with the transition matrix that contains information on population dynamics. By repeated multiplication of the transition matrix with a distribution vector of the abundances of the classes, the population growth rate converges asymptotically to a constant that equals the dominant eigenvalue λ of the matrix (Caswell 1989). Fecundity was calculated assuming a post-reproductive event as $F = s_j \times f_j$ (Morris & Doak 2002), where s_j = individual survival in class j, and f_j = number of seedlings divided by number of adults in class j. We arbitrary weights from 0.4 for Small Adults and 0.6 for Adults according to their sizes they can contribute in different ways to species reproduction. As there were no transitions for saplings, sub-adults and small adults to other size classes, minimal artificial transitions of 1% were introduced in the model to maintain an uninterrupted life-cycle.

RESULTS
Sub-population patterns

C. echinata sub-populations showed aggregated distribution patterns that were most evident on forest edges. The centre of the large fragment (CF) and the small fragment (SF), despite contrasting densities (Fig. 1; Table 3), showed Morisita's Standardized Dispersion Indexes of 0.036 and 0.024 respectively, which indicate at a local scale a tendency to a random distribution pattern. However, the more impacted edge sites (edge of the large fragment, EF, and hillside fragment, HF) showed indexes of ca. 0.2 (highly aggregated), probably due to high seedling densities forming small clumps.

The size structure of the sub-populations was based on frequency distribution of individuals per basal diameter (bd) class and ranged from a reversed-J pattern at the edge sites (SF, HF and EF) to a U-pattern in the centre of the larger fragment (CF), where no saplings were found (Fig. 1). Interestingly, the two edge sites subjected to more man-made impact (SF and HF) showed a higher proportional reduction in sapling density than the edge of the less impacted fragment (EF). Similar size structure patterns were found for height (data not shown). Seedlings represented 96.7% (ca. 800/0.1 ha) of the SF sub-population probably due to the reproductive performance of four local adults that produced ca. 9.0 seedlings/m² in November 1997 (Table 2). These adults apparently did not differ in basal diameter (bd) from the adults at other sites (Table 3). However, LF and EF had 13 (maximum bd of 350 mm and basal area of 0.09 m²) and 19 (maximum bd of 382 mm and basal area of 0.11 m²) adults respectively while SF and HF had only 4 (maximum bd of 780 mm and basal area of 0.40 m²) and 8 (181 mm and 0.02 m² respectively) adults (Fig. 1). Differences between seedling diameter size classes were marked (Table 3) probably because of the contrasting densities. SF, HF and CF saplings showed similar mean bd.

Plants at the more impacted sites (SF and HF) showed several mechanical injuries (Table 1) and SF had the highest proportion of
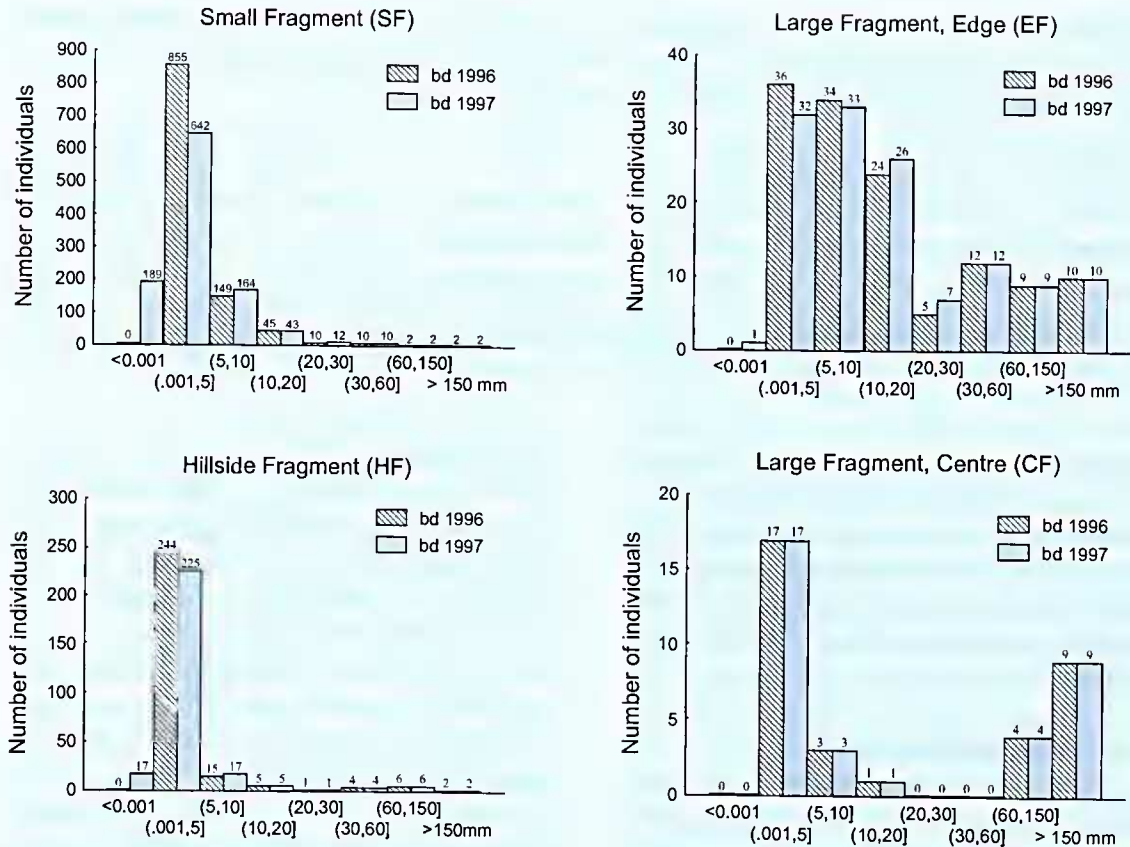
Figure 1 – Frequency distribution of plant basal diameters in sub-populations of *C. echinata* in four distinct forest fragments: Small Fragment (SF), Hillside Fragment (HF), Large Fragment, Edge (EF) and Large Fragment, Centre (CF).

Table 1 – Number of individuals (n), mortality and summary of mechanical injury in sub-populations of *C. echinata* in four distinct forest fragments at Cabo Frio region: Small Fragment (SF), Hillside Fragment Edge (HF), Large Fragment, Edge (EF) and Large Fragment, Centre (CF). * only seedlings died.

Site	n 1996	n 1997	Mortality* (%)96/97	Broken Stems 96/97	Sand burial 96/97	Resprouts 1996	Man-made cuts 96/97
SF	1074	885	17.5	87 (9.8%)	56 (6.3%)	40 (4.5%)	1 (0.1%)
HF	277	260	6.1	6 (2.3%)	2 (0.7%)	0	1 (0.3%)
EF	130	129	0.7	5 (3.8%)	0	6 (4.6%)	3 (2.3%)
CF	34	34	0	2 (5.8%)	0	2 (6.8%)	1

Table 2 – Density of *C. echinata* seedlings germinated in November 1997, after a reproductive event, in four sub-populations at distinct sites at Cabo Frio region.

Site	Means ± SE of seedlings/m²(n=10)	higher density sample[a]
Small Fragment	9.0 ± 2.3	24
Hillside Fragment	0.3 ± 0.1	1
Large Fragment, Edge	0.0 ± 0.0	0
Large Fragment, Centre	0.1 ± 0.1	1

[a]number of individuals in the sample quadrat (1x1m) with higher density

Table 3 – Mean ± SE (n) of basal diameters of *C. echinata* seedlings, saplings and adults in four distinct sub-populations at Cabo Frio region: Small Fragment (SF), Hillside Fragment (HF), Large Fragment, Edge (EF) and Large Fragment, Centre (CF).

Size class	SF	HF	EF	CF	F
Seedling	4.2±0.1 (858) a	3.1±0.1 (246) b	7.88±0.46 (90) c	4.47±0.62 (21) ab	55.82*(p<0.000)
Sapling	30.5±1.9 (23) a	39.8±5.5 (6) a	36.50±2.67 (20) a	—	2.57 (p<0.087)
Adult	270.5±171.0 (4) a	115.9±15.0 (8) a	183.5±20.1 (19) a	223.3±30.5 (13) a	1.59 (p<0.206)

The *F*-test marked values indicate significant difference between means of each group. Along each line means followed by the same letter indicate no significant differences according to Spojtvoll/Stoline Tukey's tests (p < 0.05).

damage; 17.5% of its seedlings died during the study period (1996-1997). Trampling by cattle and sand burial were possibly the main mortality causes in the understory. The sub-populations on large and less impacted fragment sites (CF and EF) apparently showed lower or absent mortality.

Whole-population patterns

The matrix analysis for one-year population dynamics after a reproductive event shows that more than 83% of individuals stay in the same class. Mortality was observed for seedling 1 and 2, sapling and adult (only one) classes. Therefore, only a few transitions to the next class were observed (1–2%), concentrated mostly in small individuals belonging to the first three classes. Regressions to smaller classes were noticed only for seedling 2 (1%) and sub-sapling (3%) classes. A small adult and an adult respectively contribute with approximately 82 and 118 new seedlings for each year. Population growth rate was about $\lambda = 1.0211$, indicating a small tendency to expand (Fig. 2). Mechanical injury patterns also suggested that density-dependent effects were small or absent, while mechanical impacts from anthropogenic sources were more frequent (Table 1).

DISCUSSION

The *Caesalpinia echinata* population studied within fragments of various sizes tends to expand by a rate of 2% after a reproductive event. This is quite surprising given the intensity of human induced fragmentation and

overexploitation of local populations since the 1500s. This seems to suggest that small adults and poles were not logged in the past, while large trunks were exported to Europe (Dean 1996). Like other long-lived tropical tree species, individuals stay for a long time in the same class with few transitions (Silvertown *et al.* 1993). Population growth rate is near one corroborating the species slow growth as expected for hardwood trees. Small growth rates were also observed in tropical rain forest tree species (Silvertown *et al.* 1993; Alvarez-Buylla 1994). Surprisingly, during the study period, we noticed one adult death, a very rare event in long-lived tree studies (Primack 1985), but we cannot know if this was due to senility or some local impact.

On the other hand, sub-populations varied in their response to fragment size and impact. Three sub-populations were subjected to considerable edge effect, and had in common a higher proportion of seedlings, as compared to saplings and adults. This was in contrast to the more similar proportion of seedlings and adults shown by the sub-population at the centre of the large fragment, away from direct edge effect. Laurance *et al.* (1998) suggest that edge effects may influence positively some recruitment rates, which in the case of *C. echinata* may be due to the higher light availability of the edge sites. Germination and early growth under cultivation (Aguiar & Barbedo 1996) and ecophysiological performance of adults in field conditions (Geßler *et al.* 2005) are favoured by higher light intensities. As
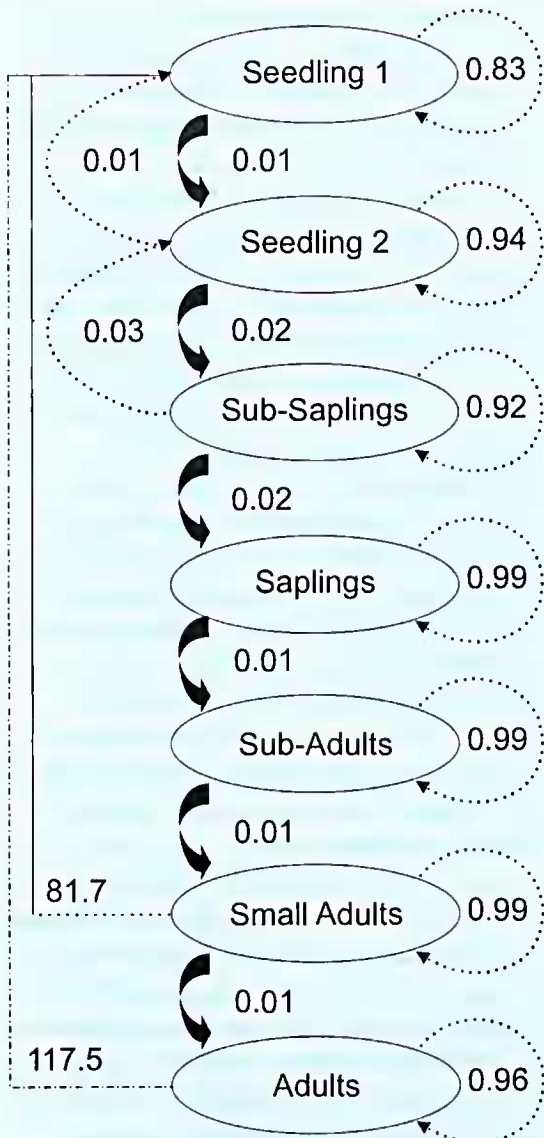
Figure 2 – Life cycle graph and estimated transition rates for the Cabo Frio region whole-population of *Caesalpinia echinata* Lam. (Brazilwood). Dominant eigenvalue λ = 1.0211 indicating that populations are expanding. Curved block arrows indicate transition to next class. A solid line indicates fecundity (seedlings produced per individual in a year). A small dotted line indicates regression to previous class and large dotted lines indicate stasis in the same class

observed by Rincón & Huante (1993), other *Caesalpinia* species also acclimate to a wide variety of light environments.

The high recruitment rates of *C. echinata* at forest edges may be an indication that success under shade could be related to gap formation. The fact that this emergent, long-lived tree is dominant in these semideciduous forests could be related to higher light availability in the understory during the dry season. These results are in agreement with Cunha & Lima (1992) who suggested that this species is a relict of old seasonal semideciduous forests, which were widespread in the drier periods of the Pleistocene.

However, there seems to be a considerable environmental sieve operating at the transition from seedling to sapling stage. This was particularly evident in the sub-population at CF, where saplings were totally absent, probably due to long periods of little or no seedling recruitment (Fenner 1985), and at the more impacted fragments (SF and HF), where seedling density was very high and the proportional individual loss from one stage to the other was higher, probably due to high man-made impact (see Laurance 2000). Supporting this, when we consider the whole population patterns, only those classes show size regressions (Fig. 1).

The fact that adult proportion in relation to seedling number was lower in the more impacted fragments (SF and HF) suggests that their reproductive value is higher. This is more evident in SF that had the largest adult plant. Larger plants tend to exhibit greater reproductive values (Horvitz & Schemske 1995; Weiner 1988), which implies sub-population differences in fecundity (see Küppers 1994).

In spite of whole population patterns indicating population regeneration and expansion, sub-populations with few fecund adults (*e.g.*, SF) may decline faster if these individuals die (Condit *et al.* 1998). Additionally, large seedling stands, as in SF, may represent an important source of genetic diversity (Sarukhán 1980). In the case studied here, the sub-population with more seedlings (858) and saplings (23) is also the one with fewer adults (4), and was located at the smallest, most impacted fragment. Thus, although this fragment had only 0.2 ha, its conservation seems of utmost importance in this area; if this fragment is excluded, the whole-population potentially declines leading to local species extinction. Furthermore, a genetic study

involving the same set of sub-populations investigated here (Cardoso *et al.* 1998; Cardoso *et al.* 2005) pointed to a considerable within-population genetic diversity in the Cabo Frio region and that the sub-populations studied are actually one genetic population with gene flow between them. Therefore, conservation initiatives for this threatened species, and possibly of the coastal plain forests of Brazil as a whole, should consider the relevance of small-sized fragments.

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